Phytolith-based environmental reconstruction from an altitudinal gradient in Mpumalanga, South Africa, 10,600 BP–present

Breman Elinor [a], Ekblom Anneli [b,*], Gillson Lindsey [c,d], Norström Elin [e]

[a] *Royal Botanic Gardens, Kew, Wellcome Trust Millennium Building, Wakehurst, Ardingly, West Sussex RH17 6TN England, UK*
[b] *Department of Archaeology and Ancient History, African and Comparative Archaeology, Uppsala University, Box 626, SE-751 26 Uppsala, Sweden*
[c] *Climate Change Leadership, Natural Resources and Sustainable Development (NRHU), Department of Earth Sciences, Uppsala University, Villavägen 16, SE-752 36 Uppsala, Sweden*
[d] *Plant Conservation Unit, Botany Department, University of Cape Town, Private Bag X3, Rondebosch 7701, South Africa*
[e] *Department of Physical Geography and Quaternary Geology, Stockholm University, 10691 Stockholm, Sweden*

ARTICLE INFO

ABSTRACT

Studying vegetation change across biome boundaries provides insight into vegetation resilience. In this study, shifts in grassland composition are reconstructed from sediments in three wetland sites across altitudinal gradient from 2128 to 897 m.a.s.l., representing a gradient from the grassland biome to the grassland/savanna boundary in the Mpumalanga region, north-eastern South Africa. Phytolith records from Verloren Valei (dated from 10,600 BP), Graskop (dated from 6500 BP) and Versailles (dated from 4500 BP) are used to reconstruct shifts in grassland composition and vegetation change. Phytolith morphotypes are used to construct environmental indices that are correlated with pollen main ecological groups, charcoal and δ13C and C/N ratio. The results are compared to available regional paleoclimate data. Both Verloren Valei and Graskop have been dominated by grassland, but Versailles show a stronger influence of bushveld/savanna pollen. Phytolith data suggest that grassland composition was stable at Versailles and Graskop, but grassland at Verloren Valei has changed significantly over time. The early Holocene was dominated by a Pooideae/Chloridoideae C3 and C4 grassland, probably a remnant of the earlier Pleistocene cool-dry conditions. After 8500 BP grassland composition changed gradually to a Chloridoideae and Panicoidea dominated C4 grassland BP, and finally a moist Cyperaceae and Panicoidea dominated C3/C4 grassland after 4000 BP. This shift possibly occurs as a delayed response to the warmer and wetter conditions of the mid Holocene optimum at this high altitude site. The results suggest that the grassland/savanna boundary has remained stable over time, indicating considerable resilience of grasslands to climate change. This resilience may be related to the turnover of species within the grassland biome, as indicated by shifts between 8500 and 4000 BP at Verloren Valei.

1. Introduction

The differential responses to environmental drivers of grasslands and savannas at the grassland-savanna boundary of Mpumalanga, South Africa, is poorly understood. So far, few paleoecological studies are available from the grassland-savanna ecotone in South Africa (but see Scott, 1990, 2016; Breman, 2010; Breman et al., 2012; Norström et al., 2009, 2018; Scott et al., 2008, Scott et al., 2012; Neumann et al., 2014; Sjöström et al., 2017; Lodder et al., 2018). Highland grassland biomes are areas of high endemism, and their history and ecology needs to be better explored for the purpose of conservation (Mucina and Geldenhuys, 2006; Neumann et al., 2014; Parr et al., 2014; Bond, 2016). In addition, historic shifts in the grassland-savanna boundary are likely to have occurred over time in response to broader climatic

and environmental changes. Pollen analysis allows broad understanding of boundary dynamics in terms of relative tree-grass abundance, but the use of phytoliths allows a more nuanced understanding of ecosystem dynamics within grassland communities. Understanding the ecological dynamics of these shifts enables a better understanding of present and future changes in the grassland biome and also the grassland-savanna boundary.

Phytolith analyses are an important tool for environmental reconstruction and have been used widely on the African continent (Bremond et al., 2008, 2017; Rossouw, 2009; Cordova and Scott, 2010; Aleman et al., 2012, 2014; Garnier et al., 2013; Neumann et al., 2009; Esteban et al., 2017; Sjöström et al., 2017; Norström et al., 2018). However, the lack of localized studies of phytolith morphotypes and C_3/C_4 pathways in modern vegetation and soils are still hampering the possibilities for environmental reconstruction and interpretation. In this paper, we use phytolith morphotypes to reconstruct environmental changes on three sites across the grassland-savanna boundary dating

from 10,600 BP to present. Three wetland sites are analyzed: Verloren Valei, (2128 m.a.s.l., grassland), Graskop (1447 m.a.s.l, grassland-.) and Versaille (897 m.a.s.l., grassland-savanna), all situated in the Mpumalanga escarpment. As a first step, we present the results from analysis of phytolith morphotypes and carbon isotopic composition (δ^{13}C) in modern grasses and sedges around the sites. In the next step, we present the phytolith assemblages in sediment cores from the three sites and compare with geochemical data (δ^{13}C and C/N ratio), fossil charcoal and pollen data grouped after ecological preferences. Phytolith indices based on broad groupings of morphotypes are used to discuss the ratio of broadleaved trees, aridity, temperature, and water stress (Alexandre et al., 1997; Barboni et al., 2007; Bremond et al., 2008, 2017; Neumann et al., 2009; Garnier et al., 2013; Esteban et al., 2017; Novello et al., 2017). The Holocene time frame and the altitudinal gradient allow us to compare vegetation responses to broader scale climatic changes as deduced from available climate proxies.

2. Materials and methods

2.1. Study area

The study is located within the summer rainfall region and grassland and savanna biomes of the northeast of Mpumalanga Province, South Africa (Fig. 1). The Mesic Highveld Grassland (MHG) bioregion dominates in the province, but Lowveld Savanna (LS) and Central Bushveld bioregions occur in the east and north of the province (Rutherford et al., 2006a). The sites are located at altitudes ranging from 897 to 2128 m.a.s.l., receiving high annual rainfall, 1100–858 mm/year, and with average minimum and maximum temperatures range from 5–8 °C to 22–29 °C (Table 1).

Verloren Valei is a large wetland in the Mesic Highveld Grassland (MHG) bioregion and more specifically the Lydenburg Montane

Grassland (LMG) hosting forbs, small trees and low shrubs, mainly C_4 grasses with a few C_3 genera (e.g. *Festuca*). The site receives both snowfall and frosts (21 days of the year) (Mucina and Geldenhuys, 2006; Harebottle et al., 2001). Graskop is a permanent freshwater marsh within the MHG bioregion and the Northern Escarpment Quartzite Sourveld (NEQS). The latter is defined by short, C_4 grassland, with high numbers of forbs, and scattered trees and shrubs. The Northern Mistbelt Forest (NMF) with species as *Podocarpus*, *Combretum*, *Syzygium* and *Olea*, occur over the cusp of the escarpment to the east, on higher elevations (1050–1650 m.a.s.l.), and in areas protected from fire and wind (Mucina and Geldenhuys, 2006). Versailles (897 m.a.s.l.), is a small sedge dominated wetland, within the Lowveld Savanna (LS) bioregion. Local vegetation is defined as Legogote Sour Bushveld (LSB) including woody species as *Sclerocarya*, *Acacia*, *Combretum*, *Erythrina*, *Antidesma* and *Olea* (Rutherford et al., 2006b). Plantation forestry (*Pinus* and *Eucalyptus* spp.) and cattle grazing dominate the present-day Versailles landscape.

2.2. Field work and sample preparation

Cores were taken using a Russian corer at the end of the dry season from the centre of each wetland basin (Table 1). The supplementary material details lithology, age depth models and methodology in detail (see also Breman (2010); and Breman et al. (2012) for Graskop and Versailles). Phytoliths were extracted from cores and prepared using standard techniques (Piperno, 2006). Pollen was extracted from cores and surface samples following standard techniques and using exotic marker grains (*Lycopodium* spores) for concentration calculation (Bennett and Willis, 2001). The pollen assemblages of each core are summarized using the main ecological groupings (e.g. grassland and shrubs, bushveld, Afromontane forest and plantations). Sums are based on percentages of terrestrial pollen sum excluding aquatics and
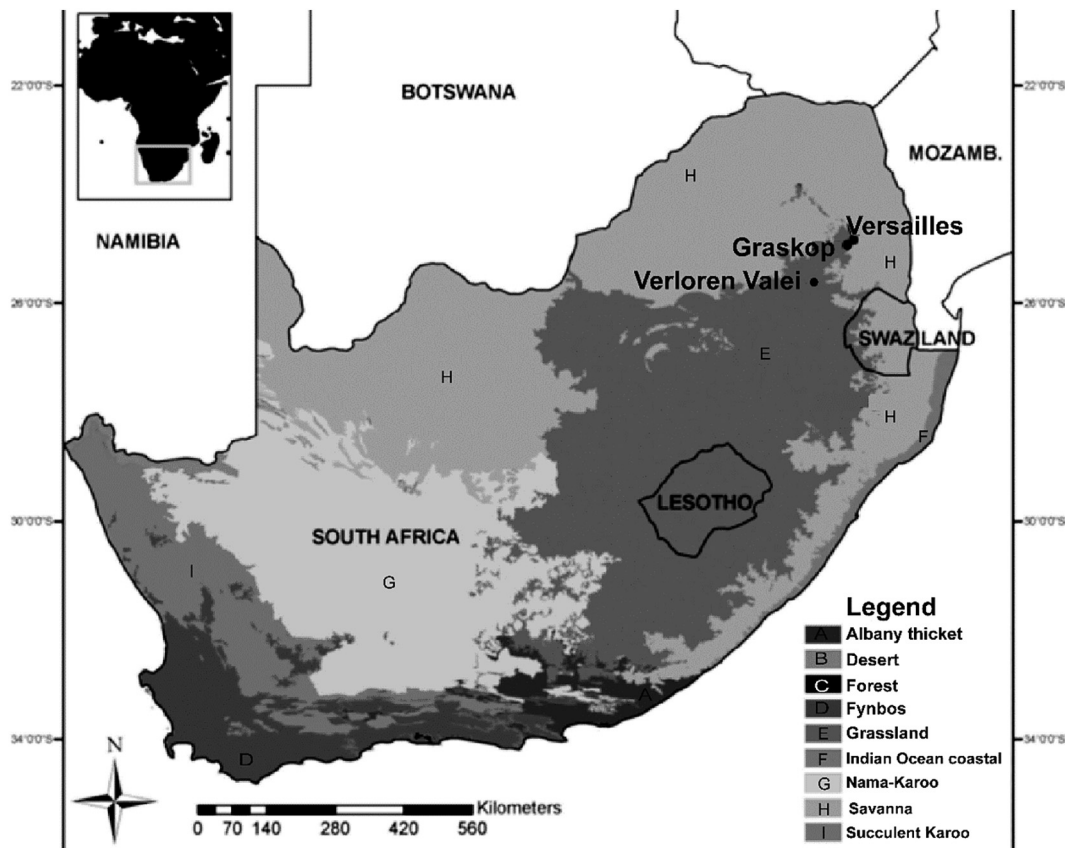

Fig. 1. Map showing the location of the Verloren Valei, Graskop and Versailles in relation to the grassland and savanna biomes. Biome vegetation map adapted from Mucina and Rutherford (2006).

Table 1
Presentation of the study sites and environmental conditions. Bioregions are the Mesic Highveld Grassland (MHG) and Lowveld Savanna (LS) (Rutherford et al., 2006a). Drainage area has been estimated based on field assessment of basin size. Climate data is based on Mucina and Geldenhuys (2006) and Harebottle et al. (2001). Local wetland vegetation data is based on vegetation surveys carried out as part of the study (Breman, 2010; Supplementary material).

Verloren Valei (2128 m.a.s.l.), MHG biorregion/Grassland		
Core depth 0–140 cm Age: 10,633–0 BP	Annual temp: 5–22 °C Annual rainfall: 858 mm/yr	Local wetland vegetation: Poaceae dominant (*Arundinella, Stiburus, Leersia, Festuca* and *Ischeamum*), with Cyperaceae (*Fuirena, Cyperus* and *Schoenoplectus*) and Asteraceae
Coordinates: S 25°17′13.1 E 30°09′08.3	Days of frost/yr: 21	(*Burkheya, Nidorella* and *Senecio*). Iridaceae and Polygonaceae also present. Of the grasses, Chloridoideae are represented by seven genera, but Panicoideae are most
Estimated drainage area c. 45.2 ha		common with 14 genera. The Andropogonaceae is represented by one genus.
Graskop (1447 m.a.s.l.) MHG bioregion/Grassland		
Core depth: 0–76 cm Age: 6500–0 BP	Annual temp: 5–25 °C Annual rainfall: 1100 mm/yr	Local wetland vegetation: Poaceae is dominant (*Andropogon, Ischeamum, Leersia* and *Stiburus*), together with Cyperaceae (*Carex, Cyperus* and *Scirpus*) and Asteraceae
Coordinates: S 24°55′13.0 E 30°50′58.4	Days of frost/yr: 3	(*Helichrysum* and *Phymaspermum*) with smaller representation of herbs. Panicoideae taxa account for the greatest amount of cover, being nine times more prevalent than
Estimated drainage area c. 1.9 ha		Chloridoideae. Chloridoideae however has a wider representation of taxa.
Versailles (897 m.a.s.l.) LS bioregion/Grassland and savanna		
Versailles Core depth: 0–259 cm	Annual temp: 8–29 °C	Local wetland vegetation: Poaceae (*Digitaria, Ischeamum, Leersia* and *Panicum*), Cyperaceae (*Mariscus* and *Schoenoplectus*) and
Age: 4432–0 BP	Annual rainfall: 949 mm/yr	Asteraceae (*Conyza*) together with herbs and shrubs from eight other families. Panicoideae taxa account for the greatest amount of
Coordinates: S 24°49′56.9 E 030°57′52.6	Days of frost/yr: 2	cover; the most prevalent Chloridoideae is *Eragrostis*. The Chloridoideae are represented by four genera, the Panicoideae by 14.
Estimated drainage area c. 1 ha		

Cyperaceae. Micro charcoal (<150 μm) (shown here as cm^2/cm^3), was counted from the pollen samples and estimated using the point count methodology (Clark, 1982; Finsinger and Tinner, 2005). Measurements of carbon and nitrogen content (C, N), as well as isotope composition (δ^{13}C, δ^{15}N) were carried out using standard techniques (Lajtha and Michener, 1994; supplementary material), here only the δ^{13}C and C/N fraction will be discussed. Thresholds for C$_3$ and C$_4$ signals in the δ^{13}C and terrestrial/aquatic component of the organic matter based on the C/N ratio are shown in the summary diagram (based on Ambrose and Sikes, 1991; Meyers, 1994; Eshetu and Hogberg, 2000; Talbot and Laerdal, 2000).

2.3. Vegetation inventory and analysis of modern reference material

Vegetation surveys were carried out at all three sites (Table 1). Poaceae and Cyperaceae specimens were collected at the three field sites in February 2008 and were used as reference material for the phytolith and stable isotope interpretation. Preparation of reference material followed Parr et al. (2001) and Piperno (2006). For isotope analyses, samples were dried at 70 °C for 24 h in a muffle furnace, and then ground to a fine powder for stable isotope analysis run at the RLAHA, Oxford University (see Appendix 1 for methodology).

Of the 26 Poaceae genera recorded in Verloren Valei, only 3 follow the C$_3$ pathway (*Bromus, Festuca* and *Koeleria*) (Table 2) and 1 can be either C$_3$ or C$_4$ (*Panicum*) (in total accounting for <5% of the total cover). The majority of Cyperaceae follow the C$_3$ photosynthetic pathway

(*Carex, Fuirena, Isolepis* and *Schoenoplectus*), and two follow the C$_4$ pathway (*Cyperus* and *Pycerus*). At Graskop, only 2 of the 18 Poaceae genera recorded use C$_3$ photosynthesis (*Agrostis* and *Alloteropsis*), and one could use either the C$_3$ or C$_4$ pathway (*Panicum*). *Agrostis* was common only in one spot; and *Alloteropsis* and *Panicum* represented less than 10% cover in the four quadrats in which they were found. At Versailles, all of the 20 Poaceae recorded, except *Leersia* (C$_3$) and *Panicum* (C$_3$ or C$_4$), follow the C$_4$ pathway. Of the five Cyperaceae genera found at Versailles only one follows the C$_3$ photosynthetic pathway (*Schoenoplectus*), the others the C$_4$ pathway (*Bulbostylis, Cyperus, Kyllinga* and *Mariscus*), but all are uncommon at Versailles.

2.4. Analyses

2.4.1. Phytolith identification and classification

Phytoliths were identified and counted using a Meiji phase contrast microscope. A minimum of 200 diagnostic phytolith types were counted in each sample (Bremond et al., 2008; Strömberg et al., 2007; Strömberg, 2009). The occurrence of charred phytoliths was recorded following Parr et al. (2001). Categorization of phytoliths followed the international code for phytolith nomenclature (ICPN working group: in Madella et al., 2005; table 3), using the reference collection and a number of identification keys (Brown, 1984; Twiss, 1992; Barboni et al., 1999; Runge, 1999; Piperno, 2006). The diagram was divided into zones using classical constrained clustering (using the paired group algorithm and the Euclidan similarity index) using PAST (Hammer et al., 2001). The morphotypes have been grouped into main groups: short cell Poaceae (subdivided into Pooid, Chloridoid, Panicoid, Arundinoid and other); long cell Pocaeae (including parallel, bulliform and point shaped); and non-Pocaeae types (including globular dicotyledon morphotypes, Cyperaceae forms and other forms). Diatoms and sponge spiculae are shown as percentages of total phytolith counts. Cyperaceae phytoliths are rare in the record at Verloren Valei; they are, however, particularly susceptible to dissolution and fragmentation (Alexandre et al., 1997; Barboni et al., 1999).

2.4.2. Environmental phytolith indices

The Broadleaved index (*globular morphotypes* (D)/*short cell grass morphotypes* (P)) (Alexandre et al., 1997), compares number of dicotyledon globular granulate with short cell Poaceae phytoliths (Aleman et al., 2012, 2013, 2014; Bremond et al., 2017; Novello et al., 2017). As the number of globular granulates were very low in all sites (<0.5%) values have not been standardized to avoid infinite values (e.g. Bremond et al., 2017), they are presented here merely as D/P.

The Aridity index (*Chloridoid*/(*Chloridoid + Panicoid*)) is based on saddle short cell types (predominant amongst Chloridoid grasses) in relation to bilobate and cross short cell types (predominant amongst Panicoid grasses) (Diester-Haas et al., 1973).

The Climatic index (*Pooid*/(*Pooid + Chloridoid + Panicoid*)) (Twiss et al., 1969) estimates the ratio of Pooid (C$_3$) phytolith short cell morphotypes (rondels) to the sum of C$_3$ and C$_4$ short cell morphotypes (e.g. rondels and trapezoids as a percentage of these types together with saddles, crosses and dumbbells).

The Water stress index (*fan-shaped phytoliths*/*short cell Poaceae phytoliths, excluding long cell types*) (Bremond et al., 2005) quantifies the amount of fan-shaped bulliform phytoliths in relation to short cell Poacea forms.

2.4.3. Comparison with other proxies

The phytolith assemblage, and in particular the indices, are compared with the pollen and charcoal record, as well as the δ^{13}C and the C/N ratio. A minimum of 350 terrestrial pollen grains were identified per sample. Percentages are based on all terrestrial taxa and undifferentiated (including degraded and indeterminate) grains. Percentages of Cyperaceae, aquatics and spores (not included in the pollen sum) were calculated on top of the pollen sum (e.g.. taxa X/pollenzum

Table 2
List of represented grasses and sedges and the δ^{13}C values for modern plant material collected at all three study sites in January 2008.

Taxa	Affiliation	Site	δ^{13}C			Determination
			Culm + leaf	Infloresence	Seed	
Leersia hexandra	Bambusoid	Verloren Valei	−26.64			C_3
Leersia hexandra	Bambusoid	Versailles	−26.11	−25.93		C_3
Carex austro-africana	Cyperaceae	Graskop	−26.49			C_3
Carex spicata-paniculata	Cyperaceae	Graskop	−26.59			C_3
Fuirena pubescens	Cyperaceae	Verloren Valei	−28.29			C_3
Isolepis fluitans	Cyperaceae	Graskop	−27.21			C_3
Schoenoplectus brychyceras	Cyperaceae	Verloren Valei	−27.59	−28.61		C_3
Schoenoplectus corymbosus	Cyperaceae	Versailles	−27.54	−27.67		C_3
Scirpus sp	Cyperaceae	Graskop	−26.58	−27.27		C_3
Alloteropsp semialat subsp. *eckloniana*	Panicoid	Graskop	−27.33			C_3
Agrostis montevidensis	Pooid	Graskop	−28.77	−25.91		C_3
Festuca caprina	Pooid	Verloren Valei	−26.16	−28.25		C_3
Festuca costata	Pooid	Graskop	−27.07			C_3
Festuca sp	Pooid	Verloren Valei	−26.29	−26.27		C_3
Koelaria capensis	Pooid	Graskop	−28.13			C_3
Aristida junciformis	Arundoid	Verloren Valei	−11.59	−10.98		C_4
Cynodon dactylon	Chloridoid	Versailles	−12.1			C_4
Eragrostis curvula	Chloridoid	Verloren Valei	−12.87			C_4
Rendlia altera	Chloridoid	Verloren Valei	−12.88			C_4
Sporobolus pectinatus	Chloridoid	Verloren Valei	−12.57			C_4
Sporobolus pyramidalis	Chloridoid	Versailles	−12.41	−12.18		C_4
Stiburus alopecuroides	Chloridoid	Graskop	−12.5			C_4
Bulbostylis sp.	Cyperaceae	Versailles	−11.15	−10.65		C_4
Cyperus rupestris	Cyperaceae	Graskop	−11.03			C_4
Kyllinga alba	Cyperaceae	Versailles	−10.07		−11.43	C_4
Mariscus congestus	Cyperaceae	Versailles	−12.24	−11.27	−11.28	C_4
Mariscus fulgens	Cyperaceae	Versailles	−10.81	−12.22		C_4
Mariscus sp	Cyperaceae	Verloren Valei	−10.79			C_4
Pycreus cooperi	Cyperaceae	Verloren Valei	−9.34			C_4
Andropogon appendiculatus	Panicoid	Graskop	−11.83			C_4
Andropogon eucocomus	Panicoid	Versailles	−12.61	−10.76		C_4
Arundinella nepalensis	Panicoid	Verloren Valei	−11.58	−10.96		C_4
Digitaria ciliaris	Panicoid	Versailles	−10.32			C_4
Digitaria eriantha	Panicoid	Versailles	−10.94	−10.8		C_4
Heteropogon contortus	Panicoid	Verloren Valei	−11.59			C_4
Imperata cylindrica	Panicoid	Versailles	−11.65			C_4
Ischeamum afrum	Panicoid	Versailles	−11.35			C_4
Loudetia simplex	Panicoid	Versailles	−11.17			C_4
Pennisetum thunbergii	Panicoid	Verloren Valei	−11.04			C_4
Themeda triandra	Panicoid	Verloren Valei	−11.91			C_4
Trichopteryx dregeana	Panicoid	Graskop	−12.82			C_4
Trichopteryx dregeana	Panicoid	Versailles	−11.84			C_4
Tristachya leocothrix	Panicoid	Verloren Valei	−10.96			C_4

+ taxa X). Comparisons are based on the main ecological pollen groups i.e., grassland herbs and shrubs, bushveld/savanna, riverine forest, Afromontane forest and plantation taxa (Table 1 in supplementary material). We also include Poaceae, Cyperaceae, *Typha*, other aquatics, and micro- and macro-charcoal. Possible correlations were tested using Detrended Correspondence Analyses (DCA) using the software PAST (Hammer et al., 2001). Single regressions were also run in Excel between categories, to estimate the coefficient of determination (R^2) and the statistical significance of the coefficient (P value).

3. Results

3.1. Verloren Valei

3.1.1. Phytoliths

Twenty-nine phytolith samples were analyzed from Verloren Valei and divided into four zones (Fig. 2). In zone 1 (10,633–9587 BP, 140–112 cm depth) bulliform type long grass cells (square and parallepipedal) are common in the base of the core (mean 35%) together with short saddles (Chloridoid) and short rondels (ungrouped short cell morphotypes). Trapeziforms (Pooid) increase progressively in the zone. Globular (dicotyledon) morphotypes are rare and continue to be so in all zones (0.1%). Charred phytoliths are also rare (2%) throughout the core. In zone 2 (9587–4868 BP, 112–56 cm depth)

bulliform long grass cells decrease (19%). Instead, Trapeziforms dominate, together with Saddle types. Short rondel morphotypes are still common. Zone 3 (4868–1265 BP, 56–24 cm depth) is marked by the increase in bilobate short shank (Panicoid) morphotypes, and to some extent cross forms (mean 19%). Trapeziforms and short saddles have the same mean representation (13%). Meanwhile, values of bulliform long grass cell types are relatively low in the zone while parallel long grass forms increase. Zone 4 (1265–0 BP, 24–0 cm depth) is defined by the continued increase in Panicoid morphotypes, mainly bilobate short shank but also cross and polylobate forms (in total 27%). Short saddle forms (Chloridoid) also increase (16%) in the zone while Trapeziforms (Pooid) decrease (9%). Cyperacaea is present in low numbers (1%). Diatoms (3%) and spiculae (0.3%) appear, and diatoms increase to 14% in the uppermost part of the zone (See Figs. 3 and 4).

3.1.2. Other proxies

In zone 1 (10,633–9587 BP, 140–112 cm depth) grass pollen values are very high (67%) in comparison to Cyperacaea (16%). Grassland herbs and shrubs are present in moderate numbers (16%) and Bushveld taxa in very low numbers (1%). Microcharcoal values are low (5 cm^2/cm^3). The C/N ratio lies over 30 suggesting a main terrestrial component. The δ^{13}C values lie below −20 in the beginning of the zone but increase towards −17 in the end of the zone, suggesting an initial main

Fig. 2. Main phytolith morphotypes identified in the Verloren Valei core and associated broad groupings of morphotypes. Summary diagram showing ecological groupings of pollen taxa, micro- and macro-charcoal, environmental indices and δ¹³C and C/N ratio.

contribution of C_3 plants but a gradually increasing contribution of C_4 pathway plants.

Zone 2 (9587–4868 BP, 112–56 cm depth) is defined by an increase in Cyperaceae (66%) and a decrease of Poacaeae (31% in the upper part of the zone). Grassland herbs and shrubs increase (26% and bushveld types minimally (2%). Microcharcoal values increase to 8 cm²/cm³ and macrocharcoal is also present in very low numbers. The C/N ratio continues to lie within the terrestrial range. The $\delta^{13}C$ values lie below −18% PBD in the beginning of the zone but rise at 8500 BP to −16% PBD which is completely within the range of C_4 vegetation.

In zone 3 (4868–1265 BP, 56–24 cm depth) Cyperaceae continues to be dominant (57%) over Poaceae (39%), and there is a decline in grassland herbs and shrubs (21%). Bushveld taxa and Afromontane taxa increase (5% and 2% respectively). *Typha* peaks at 13%, together with an increase in aquatics and monolete/Trilete spores. Microcharcoal values decrease markedly (8 cm²/cm³) and there is also a small decline in macrocharcoal (22 fragments). Values of $\delta^{13}C$ and C/N values fall to below −20 and 17, respectively, suggesting a stronger influence of aquatic plants and C_3 plants to the organic matter.

Zone 4 (1265–0 BP, 24–0 cm depth) shows continued low C/N ratio suggesting a continued strong influence of aquatics in the organic matter component. However, $\delta^{13}C$ values decrease below −20 in the zone suggesting a stronger influence of C_4 plants, particularly in the uppermost part of the zone. Poaceae increase over Cyperaceae in the upper part of the zone. Grassland herbs and shrubs as well as shrubland decrease (21% and 5%, respectively), while Afromontane taxa are present in very low numbers. Plantation taxa occur in the top of the zone. Total macrocharcoal shows very high values particularly in the uppermost part of the zone, but microfossil charcoal show similar numbers as before (7 cm²/cm³).

3.2. Graskop

3.2.1. Phytoliths

As the top 18 cm dates to after 1950 the top of the sequence has negative BP dates. A total of 12 levels were counted and four zones identified. Zone 1 (6533–2366 BP, 56–76 cm depth) is dominated short shank bilobate short cell Poacea (Panicoid) (26%) and by long cell bulliforms (22%). Saddle forms (Chloridoid) are also common (11%). Non-grass forms are very rare, globular (dicotyledon) morphotypes occur with a mean percentage of 0.2% (all zones). Charred phytoliths are present in low numbers (2.6%). In zone 2 (2366–317 BP, 36–56 cm depth) bilobate short shank types (36%) continue to increase over bulliform long cell Poaceae phytoliths (12%). Globular (dicotyledon) morphotypes are still rare but increase to around 0.4%. Charred phytoliths increase slightly (3.8%). Zone 3 (317 to −36 BP (e.g. 1986 AD), 4–36 cm depth) is characterized by the decline in short shank bilobate short cell Poacea (21%) and long cell Poaceae also displays relatively low numbers (24%). There is an increase in square Typhus morphotypes (6%). Charred phytoliths decrease slightly (2.4%). Zone 4 (−36 to −48 BP (e.g. 1986–1998 AD), 0–4 cm depth) shows a marked increase in diatoms (15%) and also marked variations in the distribution of grass morphotypes. Short shank bilobate morphotypes first decrease (12%), while Pooid and Arundinoid type forms increase. Bilobate short Poaceae cells increase again in the uppermost level (28%) while long cell Poaceae continue be present in low numbers (16%).

3.2.2. Other proxies

Zone 1 (6533–2366 BP, 56–76 cm depth) has very high pollen concentration values (63⁶/cm³). Percentages of Poaceae are high (57%) in comparison with Cyperaceae (11%). Grassland taxa (24%) and Afromontane taxa are well represented (11%) but bushveld and forest species only in low numbers. Monolete and trilete spores are present in very low numbers (1%). Microcharcoal influx is extremely high (528 cm²/cm³) and increases in the top of the zone. Macrofossil charcoal

is very rare (44 fragments). The C/N ratio lies over 30 suggesting a main terrestrial component. The $\delta^{13}C$ values decrease from c. −20 to −18 suggesting a main contribution from C_4 pathway plants.

Zone 2 (2366–317 BP, 36–56 cm depth) shows continued very high influx of microcharcoal values (898 cm²/cm³) in the bottom of the zone together with macrofossil charcoal (341 fragments). Pollen concentration continues to be high (47⁶/cm³). Poaceae and other grassland taxa decrease (56% and 20%, respectively) while Cyperaceae increase slightly (18%). Afromontane forest taxa also decline (11%), while bushveld and forest taxa show very low values. Monolete and trilete spores increase slightly. The C/N ratio continue to lie above 30 but $\delta^{13}C$ increases in the beginning of the zone to values higher than −18 and continue to lie fully within the C_4 pathway plant range.

In zone 3 (317 to −36 BP i.e. 1986 AD), 4–36 cm depth) both Poaceae and Cyperaceae decline progressively in the zone. Percentages of Afromontane taxa are similar to zone 2 (11%) while plantation taxa occur with high values (14%) from 100 BP. Microcharcoal influx is very low (14 cm²/cm³) and pollen concentration also decreases (24⁶/cm³), but macrocharcoal values continue to be high (858 fragments). The zone shows a dramatic change in C/N ratio falling below 20 from 159 BP, suggesting a mix of aquatic and terrestrial components to the organic matter. The $\delta^{13}C$ values from the same time fall between −20 and −21, closer to the C_3 pathway range. Values increase again at the very top of the core.

In zone 4 (−36 to −48 BP i.e. 1986–1998 AD, 0–4 cm depth) Poaceae (52%) and other grassland taxa (17%) occur in moderate numbers, the former increasing slightly compared to previous zone. Forest taxa percentages increase (2%) but Afromontane taxa values are low (4%). Plantation taxa continue to be common (14%). Macrocharcoal decline but continues to be high (604 fragments), but microcharcoal influx is very low (5 cm²/cm³) as is pollen concentration (13⁶/cm³). The C/N ratio of c. 16 suggest a continued mix of aquatic and terrestrial components to the organic matter while $\delta^{13}C$ values lies around −24 which is close to the C_4 pathway range.

3.3. Versailles

3.3.1. Phytoliths

Phytoliths were analyzed in 15 levels and divided into three zones. Zone 1 (3680–4457 BP, 180–259 cm depth) is marked by high values of long cell bulliform types (38%). Panicoid types (15%) are also common, dominated by bilobate short shanks and cross morphotypes. Globular forms are present in low numbers (0.2%), as are also diatoms (1%) and charred phytoliths (2%).

Zone 2 (1599–3680 BP, 80–180 cm depth) is characterized by a marked decrease in long grass cell bulliforms (21%). Parallel long grass cell forms are also relatively common (16%). Short cell Pocaeae Rondels increase (16%) and Bilobate short shank morphotypes continue to be common (14%). There is also a slight increase in Trapeziform (Pooid) morphotypes (10%). Cyperacaeae forms increase slightly to 2%. Charred phytoliths (3.1%) peak in the uppermost level of the zone. Zone 3 (0–1599 BP, 1–80 cm depth) is dominated by Panicoid types (26%), of which Bilobate short shank morphotypes are most common. Chloridoid types, mostly short saddles, are also common (11%). Poaceae long cell bulliforms (33%) (e.g. square, parallepipedal and long Poaceae parallel forms) are also common. Cyperacaeae forms occur in very low numbers (3%) but Globular (dicotyledon) morphotypes shows higher values than before (0.5%).

3.3.2. Other proxies

Pollen concentration is high in zone 1 (12⁶/cm³) and increases in zone 2 (17⁶/cm³). The uppermost zone has a similar pollen concentration to zone 1 (12⁶/cm³). Comparison between pollen concentration, and microcharcoal influx, and of number of charred phytoliths against microcharcoal, does not show any correlation.
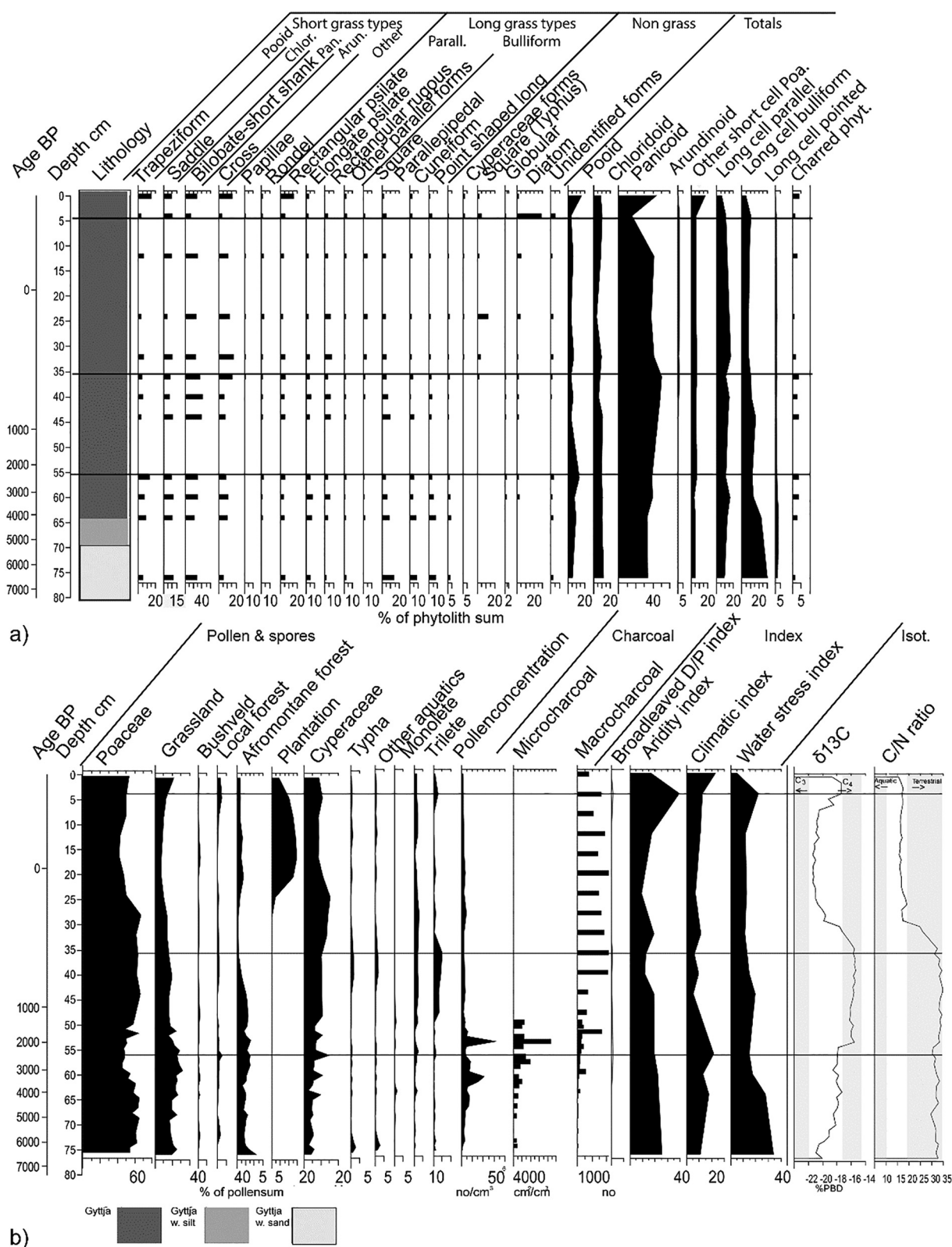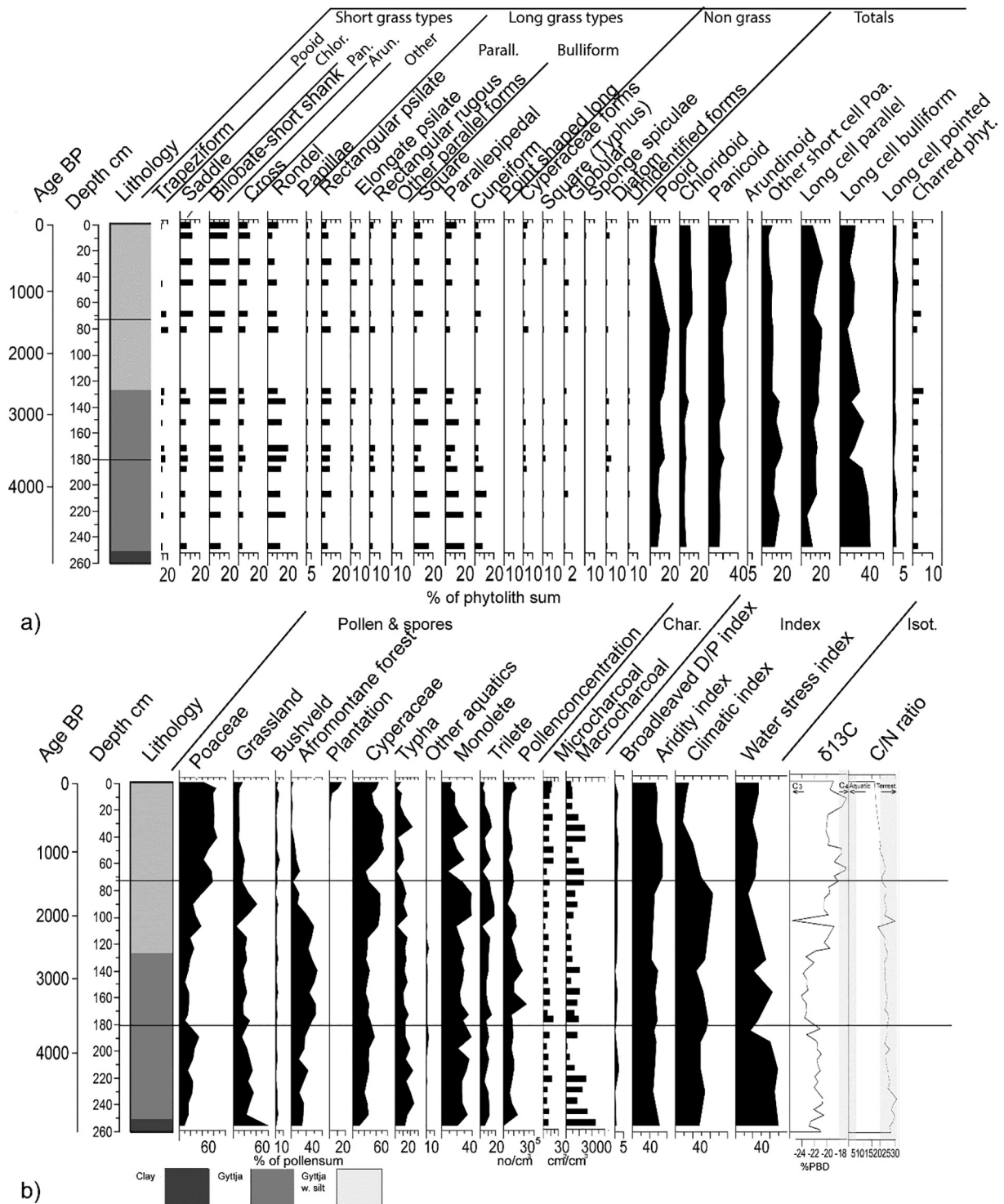
Fig. 3. (a) Main phytolith morphotypes identified in the Graskop core and associated broad groupings of morphotypes. (b) Summary diagram showing ecological groupings of pollen taxa, micro- and macro-charcoal, environmental indices and δ¹³C and C/N ratio.

Zone 1 (3680–4457 BP, 180–248 cm depth) is defined by high values of Poaceae (55%) and high, but variable values of Cyperaceae (41%). Grassland herbs and shrubs and Afromontane taxa are uncommon (14% and 4%, respectively). Plantation taxa (2%) occur in the very top of the core. Monolete spores decline (21%). Both microcharcoal influx and macrocharcoal numbers increase (8.67 cm²/cm³ and 1296 fragments, respectively). The C/N ratio suggest a terrestrial origin of the organic matter with values above 25. The δ¹³C lies around −22 suggesting influence from a mix of C₃/C₄ pathway plants.

Fig. 4. (a) Main phytolith morphotypes identified in the Versailles core and associated broad groupings of morphotypes. (b) Summary diagram showing ecological groupings of pollen taxa, micro- and macro-charcoal, environmental indices and δ13C and C/N ratio.

Zone 2 (1599–3680 BP, 80–180 cm depth) shows moderate values of Poaceae (21%) and Cyperaceae (25%). Grassland herbs and shrubs are dominant (60%) in the beginning of the zone but decreases to values around 15%. Percentages of Afromontane taxa are high (15%) but low for Bushveld taxa low (1%). Typha (17%) has its highest representation in this zone. Monolote fern spores (38%) are well represented throughout the core, and Trilete spores (ferns and mosses) are also common. Macrofossil charcoal is present with very high numbers (1558 fragments) early in the zone, while microcharcoal influx is relatively low

(6.71 cm²/cm³). The C/N ratio still indicates a terrestrial origin of the organic matter with values around 25. The δ13C percentages moves increase to −20 suggesting a gradual change to a higher influence of C4 plants.

In zone 3 (0–1599 BP, 1–80 cm depth) both Poaceae and Cyperaceae show low values in the beginning of the zone (20% and 31%, respectively) but increasing values towards to the top. Grassland herbs and shrubs are present in moderate but variable amounts (22%). Afromontane taxa increase significantly in the zone (26%). Monolote

spores continue to be well represented (28%). Micro- and macrocharcoal is present in moderate numbers (6.59 cm^2/cm^3 and 949 fragments, respectively). The C/N ratio lies around 20, which still suggests that the main organic component is terrestrial. Meanwhile the δ^{13}C has values between -20 and -18 suggesting a high influence of C$_4$ plants.

3.4. Regression and correspondence analyses

Regressions were made between pollen concentration, charcoal influx and charred phytoliths. For Verloren Valei there is a low coefficient of determination between microcharcoal influx and pollenconcentration R^2 = 0.228, P value <.001, while charred phytoliths has no significant coefficient over microcharcoal. For Graskop and Versailles there is no significant coefficient between either of these categories.

The Verloren Valei RDA place the Aridity index closely with the C/N ratio (Fig. 6) and a regression shows a very strong positive coefficient (R^2 = 0.7753, P value <.001). In axis 2 and 3 the Aridity index is correlated with Pocaeae (R^2 = 0.4338, P value <.001). The Broadleaved (D/P) index is weakly correlated with Bushveld/savanna pollen taxa (R^2 = 0.1409 in a regression), though the statistical significance is low (P value 0.051). The Climate index shows some correlation with the δ^{13}C (In regression the coefficient is positive R^2 = 0.2649, P value 0.005), and the C/N ratio (R^2 = 0.26488, P value 0.005). The Poaceae/Cyperaceae ratio is positively correlated against the Aridity index (R^2 = 0.4867, P value >.001) and also more weakly with the Climate index (R^2 = 0.1386, P value >.001) and the Water stress index (R^2 = 0.1910, P value 0.02).

For Graskop there are fewer samples (13) with all proxies represented. The DCA of Graskop, axis 1 and 2 place the Climatic index in proximity to the C/N ratio (The coefficient in regression was weakly positive R^2 = 0.1064, but with low significance (P value 0.3). The correlation between Pocaeae and the Aridity index shown in Verloren Valei is absent in Graskop. Water stress index falls close to aquatics for axis 2 and 3 but the correlation was not significant when tested in single regression. The Broadleaved (D/P) index is correlated with forest taxa both in the DCA and in a regression (R^2 = 0.4842, P value 0.01). When the Poaceae/Cyperaceae ratio is tested against the indices the Water stress index shows a strong correlation (R^2 = 0.4019, P value 0.03).

The Versailles core also has few data points with all proxies represented (11). The DCA, axis 1 and 2, correlates the Water stress index and Climate index to the C/N ratio (R^2 = 0.3255, P: 0.03 and R^2 = 0.5123, P: 0.003) while the Aridity index shows a weak negative correlation (R^2 = 0.1187, P: 0.2) with the C/N ratio. The Broadleaved (D/P) index shows no significant correlation with Bushveld/savanna pollen taxa. The Climate index in the DCA axis 2 and 3 shows some correlation with the δ^{13}C but this correlation is not significant (R^2 = 0.2036, P: 0.09). The Poaceae/Cyperaceae ratio is correlated with the Aridity index (R^2 = 0.3582, P: 0.02) and negatively correlated with both the Climatic index (R^2 = 0.15, P: 0.15) and the Water stress index (R^2 = 0.1463), though with low statistical significance (P: 0.16).

4. Comparison with other proxies and the paleoclimate record

4.1. Deposition and representation

The local wetland environment may be highly influential for phytolith deposition (Aleman et al., 2013), but the phytolith assemblage can also be representative of more regional scale conditions (Livingstone and Clayton, 1980; Fredlund and Tieszen, 1994; Boyd, 2005; Piperno, 2006; Fredlund et al., 1998). Aleman et al. (2014) compared phytolith influx, charcoal influx and charred phytoliths, suggesting that phytoliths were transported by wind with ash clouds. Lacking concentration data for the phytoliths we compared microcharcoal influx with presence of

charred phytoliths. None of the cores showed a significant coefficient of determination in the regression between these two categories.

The δ^{13}C values and C/N ratio provide information on the composition of the organic matter, which is important for the understanding of depositional process (Fig. 5). For Verloren Valei, the C/N ratio lies over 30 in the lower part of the core suggesting a mainly terrestrial component (Talbot and Laerdal, 2000) until 4000 BP after which C/N declines to around 10, suggesting a stronger aquatic component (Fig. 5). The C/N ratio of the Graskop core is strongly terrestrial but with a mix of terrestrial and aquatic in the very top of the core. Meanwhile, the C/N ratio at Versailles progressively changes from being strongly terrestrial, towards a mixture of terrestrial and aquatic in the uppermost part of the core. Thus, only at Verloren Valei, a strong local aquatic signal was detected (after 4000 BP), otherwise the organic matter is mainly terrestrial.

The Aridity index can be strongly biased by the contribution of local aquatic vs mesophytic grasses (Novello et al., 2012; see also Aleman et al., 2013). The Aridity index is calculated on the basis of the values of Panicoideae and Chloridoideae grasses. The index may be overestimated based on the fact that Panicoideae grasses may also produce saddle morphotypes, a typical Chloridoideae form (Bremond et al., 2005). Moreover, Arundinoid grasses may produce phytoliths characteristic of both Panicoideae (e.g. *Aristida*, *Stipa*) and Chloridoideae (e.g. *Phragmites*). In our case, Phragmites-type phytoliths were present only in very low numbers, and they were not included in the index (see also Barboni et al., 1999). Panicoideae grasses are not growing in the investigated wetlands and the Arundinoid subfamily is rare at all three sites (Table 2). Historically, conditions may have been different, as Panicoid type morphotypes are common in all of the cores and they also increase after 4000 BP both at Verloren Valei and Graskop.

The Climatic index potentially distinguishes the grasses with a C$_3$ photosynthetic pathway from those that follow a C$_4$ pathway (Parker et al., 2004). Generally, C$_3$ Poaceae are rare in the summer rainfall region, but can occur at altitudes where conditions are cooler and wetter (Vogel et al., 1978). The sampled sites are presently dominated by C$_4$ grasses (Table 2) but *Sporobolus* (C$_4$), is common at the study sites and produces Pooid type phytoliths (e.g. rondels) although being a Chloridoideae grass. This could potentially overestimate the Climatic index. Pooid morphotypes are also very common in all cores also in the top sediment where we know from the vegetation inventories that there are very few Pooideae grass growing today. Thus, the presence of Pooid phytolith morphotypes in the fossil record is likely to be an effect of redundancy, but a stronger element of Pooideae grass in the early Holocene should also be considered as discussed below.

4.2. Correlation of indices with other proxies

The strongest correlation in the dataset is between the C/N ratio and Aridity index, Pocaeae/Cyperaceae ratio and also to some extent δ^{13}C. The δ^{13}C in OM could, in addition to C$_3$/C$_4$ dynamics, be related to the degree of moisture stress experienced by the terrestrial plants (Cernusak et al., 2013) Thus, in the studied cores, there seem to be a coupling between aridity, terrestrial OM (C/N), grass dominance over sedges, and an increase in C$_4$ components and/or moisture stress (δ^{13}C).

Though the total numbers of dicotyledon globular granulates are very few, the Broadleaved (D/P) index does correlate with bushveld/savanna and forest taxa in many of the cores (in general the D/P index is known to underestimate woody cover (Boyd, 2005; Hyland et al., 2013)). Thus, both the Broadleaved (D/P) index and the pollen record suggest a predominance of open grasslands in Verloren Valei since 10,600 BP and Graskop since 6533 BP. Versailles, however, has a stronger presence of bushveld/savanna pollen taxa and also of Afromontane pollen taxa. The Broadleaved (D/P) index is also slightly higher here.
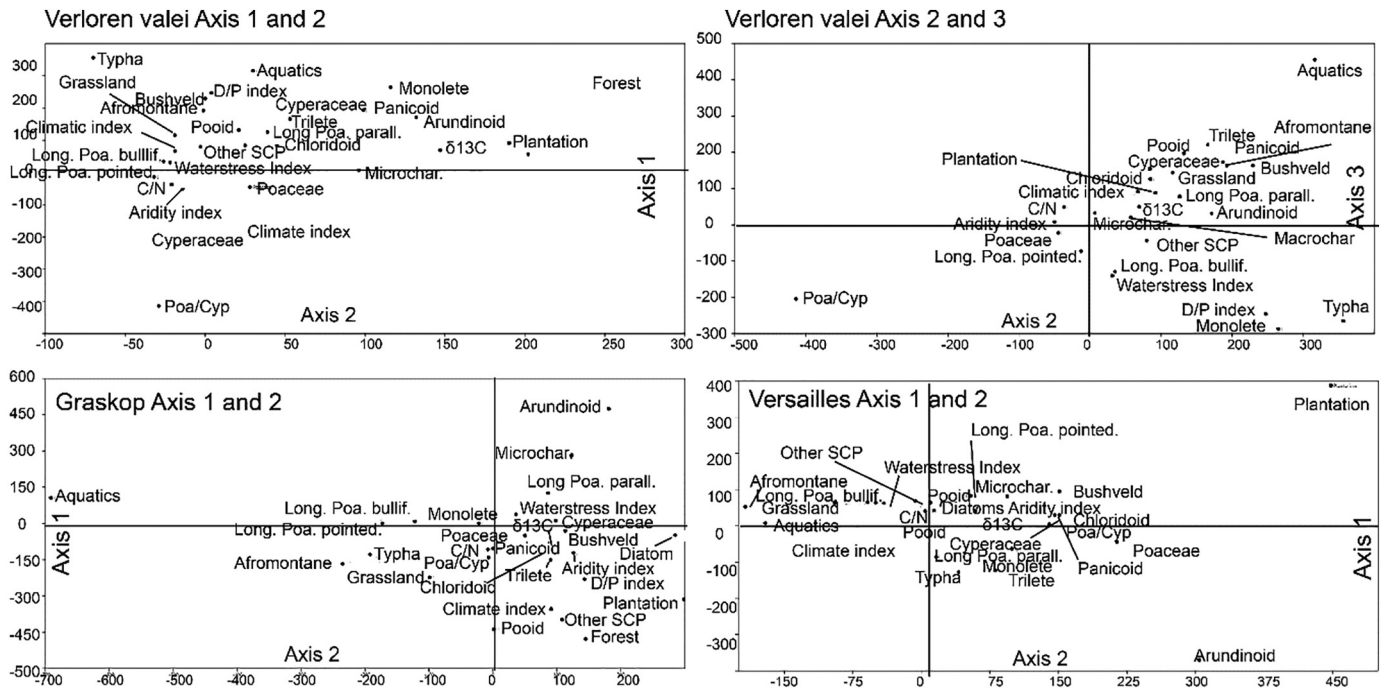
Fig. 5. Detrended correspondence analyses of the three sites.

4.3. Comparison with the climate record

4.3.1. 10,000–8500 BP

In the summer rainfall region, colder temperatures were associated with relatively dry conditions based on available paleoclimate records

(Lee-Thorp et al., 2001; Holmgren et al., 2003; Neumann et al., 2014; Scott, 2016). At Verloren Valei, the Broadleaved (D/P) index and pollen data suggest an open grassland over this phase. The high Aridity index suggests overall drier conditions, based on a large contribution of Chloridoid phytolith types over Panicoid. Chloridoid grasses typically
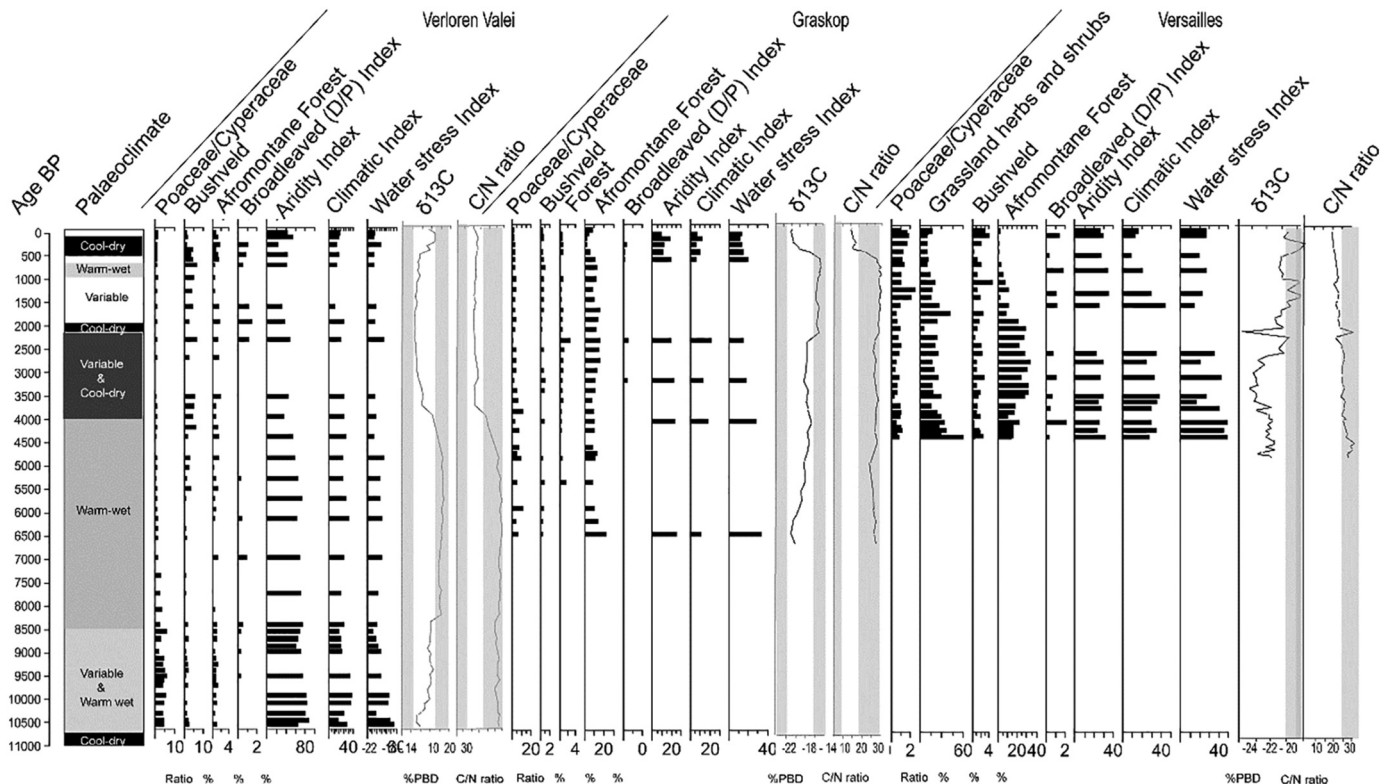

Fig. 6. Summary diagram showing the main paleoclimatic trends (Lee-Thorp et al., 2001; Holmgren et al., 2003; Scott, 2016), Poacea/Cyperaceae ratio, bushveld and afromontane pollen taxa in relation to the environmental indices and δ¹³C and C/N data for the three sites.

are xerophytic (short) grasses adapted to drier conditions (see also Scott et al., 2012), while Panicoid grasses are mainly tall grasses better adapted to humid conditions. The threshold value between the grass systems, using the Aridity index, have been suggested to lie below 30% for tall grass systems in tropical Africa (Alexandre et al., 1997), and 20% in West Africa (Bremond et al., 2005). At Verloren Valei, the average Aridity index value for the whole core is 54%, and 73% for the early Holocene period. This is due to the dominance of Chloridoid forms in the beginning of period suggesting high presence of drought adapted grasses, close to the values presented for Sahelian grassland/woodland (Novello et al., 2012). Chloridoideae grasses have been correlated with cool-dry conditions elsewhere in the grassland region (see also Scott et al., 2008; Scott et al., 2012; Scott, 2016). In addition, the values of Pooid morphotypes are relatively high. Many Pooideae grasses are C_3 pathway plants (Tieszen et al., 1979; Livingstone and Clayton, 1980; Gibbs Russell, 1986; Cordova and Scott, 2010) and the presence of Pooideae may help explain the strong C_3 signal in the beginning of the core.

The Climatic index values are c. 40% in the beginning of the core. In intertropical Africa values of less than 40% are common in the C_4 dominated grassland on mid elevations while C_3 dominated grasslands on higher elevations (and with colder temperatures) usually have percentages above 60% (Barboni et al., 2007). The Climatic index in combination with the $\delta^{13}C$ does suggest some influence of C_3 grasses in our study area during this period. The Water stress index is based on the presence of bulliforms, which require greater amounts of silica carrying water to form compared to short cell types. High percentages in the Water stress index potentially indicate an increase in transpiration and/or duration of water stress due to low water availability (Bremond et al., 2005). At Verloren Valei Water stress percentages are suspiciously high (37%), e.g. similar to what has been reported in Sahara and Sahel (Bremond et al., 2005). Percentages decline in later periods however.

4.3.2. 8500–4000 BP

In the period 8500–c.4000 BP the summer rainfall region of southern Africa experienced warm conditions and an overall increase of rainfall (Lee-Thorp et al., 2001; Holmgren et al., 2003, Holmgren et al., 2012; Scott and Lee-Thorpe, 2004; Norström et al., 2009; Scott et al., 2012, Scott, 2016). Our study sites show significant changes in the composition of the organic matter with continued terrestrial dominance but a shift to $\delta^{13}C$ values below −17‰ which is within the C_4 pathway range (Meyers, 1994). In general, the Climatic index lies around 31% and the water stress index also displays lower percentages than before (24%). The Aridity index continues to display very high values (60%), but declines as Panicoid phytolith forms increase over Chloridoid ones. The base of the Graskop core dates to this period (6533 BP) but only has one level representing the period. The Aridity index at Graskop (25%) is significantly lower than in Verloren Valei, and within the range of the tall grass systems in other parts of the continent. The Water stress index (c. 33%) suggests that water stress throughout the sequence was low, progressively decreasing towards the upper part of the sequence. Meanwhile, the Climatic index values are very low (c. 14%) also supporting warmer conditions. The warming period is ended by the onset of cooler conditions. Some evidence of cooling is present already from 5500 to 6000 BP with variable moist/warm conditions 4300–3200 BP (Lee-Thorp et al., 2001; Holmgren et al., 2003, 2012). Scott et al. (2012) places the ending of the Holocene optimum at 4000 BP, which is supported by the data presented here.

4.3.3. 4000–2000 BP

Paleoclimate proxies suggest that the period 4000–2000 BP was variable but overall cooler and drier (Scott et al., 2012). 4000 BP marks an increase in Panoicoid grasses at both Verloren Valei and Graskop. The change is most distinct in the Verloren Valei core. The Climatic index lies around 30% but the water stress percentages are relatively low (22%). The Aridity index values are still very high (c. 50%) but decline

markedly in comparison to the previous period. The C/N record with values below 20, suggest increasing influence of aquatic organic matter. The shift in $\delta^{13}C$ to <− 20 suggest a shift in grassland composition again, from C_4 dominance towards a mix of C_3 and C_4 plants. The isotope shift could in part be related to the stronger aquatic influence (Cyperaceae and *Typha* pollen also increase), but it is also related to a change in vegetation with more C_3 herbaceous, shrub, tree and bushveld taxa. For Graskop, the Aridity index continues to lie around 30%, close to the suggested threshold value between short and tall grass systems. The Climatic index lies at 15% which suggests a continued and strong dominance of C_4 grasses, supported also by the $\delta^{13}C$ values that lies around − 17‰ i.e. within the C_4 range. The values for the Water stress index at 12% are low, and do not support the presence of droughts or water stress. Versailles, contrary to the other sites had open water conditions throughout the last 4500 years as suggested by the high presence of diatoms. The average percentage of the Aridity index lies at 26% (again within the range of the suggested threshold between short and tall grass systems). However Pooid phytolith types, affect the Aridity index, and may include some Chloridoideae grasses (Mulholland, 1989) as already discussed above. The Climatic index lies at 31% suggesting a dominance of C_4 grasses, while $\delta^{13}C$ is suggesting a C_3 signal (ca − 22 ‰), Similar as in Verloren Valei, $\delta^{13}C$ is probably influenced by an increase in non-grassy vegetation (C_3 trees, shrubs, sedges), in contrast to the Climatic index which is only affected by grass dynamics. The values for the Water stress index are initially very high (49%–40%) but decrease after 3800 BP, there is, however, a peak (35%) at 2900 BP. A marked period of dryness is suggested to have taken place at 2000 BP, connected also to an overall expansion of C_4 grasses (Holmgren et al., 2003; Scott et al., 2012). This event is not clearly distinguishable here, perhaps as a result of low sampling and age depth resolution in our data. Alternatively, the duration of the drought event was too short to be reflected here. Possibly that the water stress peak at Graskop correlates to the 2000 BP drought.

4.3.4. 2000 BP to present

After 2000 BP conditions were variable but overall humid/moist conditions prevailed with shorter episodes of cool-dry and warm-wet conditions (Holmgren et al., 2012; Norström et al., 2018a; Humphries et al., 2016) until c. 1250–800 BP when conditions became overall warmer and wetter (Lee-Thorp et al., 2001; Holmgren et al., 2003, 2012; Norström et al., 2018b). From 2000 BP, there is an overall decline in the Climatic and Aridity indices linked with a continued increase of C_4 Panicoid grasses. In Verloren Valei, $\delta^{13}C$ values suggest a continued mix between C_3/C_4 plants. From c. 500 BP there is an increase in the Climatic and Aridity indices, linked with an increase of Chloridoid types over Panicoid. Similarly, an increase in Aridity index is reported in lake sediments in southern Mozambique around this time (Norström et al., 2018b). At c. 300 BP there is an increase in Bulliforms (and also other long cell morphotypes) and as a result the Water stress index increase to 28%. Possibly this can be related to the overall cool dry period occurring from 800 or 600 BP to 200 BP with the most extreme conditions during 300 BP (Lee-Thorp et al., 2001; Holmgren et al., 2003, 2012; Sundqvist et al., 2013). Throughout the whole period from 500 BP to present C_4 plants also become more prominent in the Verloren Valei core. In Graskop a switch from C_4 dominated vegetation to a mix of C_3/C_4 plants can also be seen but from c. 500 BP. At Versailles, which has had a higher water table over time, the $\delta^{13}C$ values show continued high influence of C_4 plants throughout the period.

5. Conclusion

Grasslands are important but neglected biodiversity conservation targets, whose history and ecology is often poorly understood. Pollen-based studies of grasslands are important in distinguishing ancient from derived grasslands, but give little insight into grassland ecology and resilience over time. The phytolith data presented here suggest

that there are no indications of major biome shifts when it comes to the savanna-grassland boundary. Overall both Verloren Valei and Graskop has been dominated by grassland over the time period of 10,600 years and 6500 years, respectively. Only the lowest savanna site, Versailles (at 897 m.a.s.l.) show a stronger influence of bushveld/savanna pollen taxa over time though numbers are continuously low and there is no indication of significant shifts in the ecotone, suggesting considerable resilience of the ecotone to climate change.

The resilience of the grassland community might result from turnover of grassland composition, within the grassland biome. Here we have suggested that the early Holocene was dominated by a Pooideae/Chloridoideae C_3 and C_4 grassland at Verloren Valei, which was probably a remnant of the earlier Pleistocene cool-dry conditions. Pooid C_3 grasslands are common in the winter rainfall region but the highest diversity of species is found in the montane areas of the summer rainfall region (Cordova and Scott, 2010). Smith et al. (2002) place the boundary limit for C_3 grasslands for southern Africa at 2300 m.a.s.l. However, this boundary limit is here suggested to have been lower.

After 8500 BP grassland composition changed gradually to a Chloridoideae and Panicoidea dominated C_4 grassland BP, and finally a moist Cyperaceae and Panicoidea dominated C_3/C_4 grassland after 4000 BP. This shift possibly occurred as a delayed response to the warmer and wetter conditions of the Holocene optimum.

The results suggest considerable resilience of grasslands to climate change as responses, historically, have been slow and with a considerable time lag in responding to climate change. However, the shifts in grassland composition at Verloren Valei at 8500 and 4000 BP could also be considered as irreversible changes and there needs to be more research to look into how such dynamics would be effected by present day and future climate change.

Acknowledgments

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.revpalbo.2019.01.001.

References

Aleman, J., Leys, B., Apema, R., Bentaleb, I., Dubois, M.A., Lamba, B., Lebamba, J., Martin, C., Ngomanda, A., Truc, L., Yangakola, J.-M., Favier, C., Bremond, L., 2012. Reconstructing savanna tree cover from pollen, phytoliths and stable carbon isotopes. J. Veg. Sci. 23, 187–197.

Aleman, J.C., Saint-Jean, A., Leys, B., Carcaillet, C., Favier, C., Bremond, L., 2013. Estimating phytolith influx in lake sediments. Quat. Res. 80, 341–347.

Aleman, J., Canal-Subitani, S., Favier, C., Bremond, L., 2014. Influence of the local environment on lacustrine sedimentary phytolith records. Palaeogeogr. Palaeoclimatol. Palaeoecol. 414, 273–283.

Alexandre, A., Meunier, J.-D., Leczine, A.-M., Vincens, A., Schwartz, D.A., 1997. Phytoliths: indicators of grassland dynamics during the late Holocene in intertropical Africa. Palaeogeogr. Palaeoclimatol. Palaeoecol. 136, 213–229.

Ambrose, S.H., Sikes, N.E., 1991. Soil carbon isotope evidence for Holocene habitat change in the Kenyan Rift Valley. Science 253, 1402–1405.

Barboni, D., Bonnefille, R., Alexandre, A., Meunier, J.D., 1999. Phytoliths as paleoenvironmental indicators, West Side middle Awash Valley, Ethiopia. Palaeogeogr. Palaeoclimatol. Palaeoecol. 152, 87–100.

Barboni, D., Bremond, L., Bonnefille, R., 2007. Comparative study of modern phytolith assemblages from inter-tropical Africa. Palaeogeogr. Palaeoclimatol. Palaeoecol. 246, 454–470.

Bennett, K.D., Willis, K.J., 2001. Tracking environmental change using lake sediments. In: Smol, J.P., Birks, H.J.B., Last, W.M. (Eds.), Terrestrial, algal and siliceous indicators. 3. Kluwer Academic Publishers, Dordrecht, pp. 5–32 Pollen.

Bond, W.J., 2016. Ancient grasslands at risk. Science 351, 120–122.

Boyd, M., 2005. Phytoliths as paleoenvironmental indicators in a dune field on the northern Great Plains. J. Arid Env. 61 (3), 357–375.

Breman, E., 2010. Pattern and process in grass-dominated ecosystems: Vegetation dynamics at the grassland-savanna ecotone in South Africa during the Holocene. Ph.D. Thesis. School of Geography and the Environment, Oxford University, Oxford, United Kingdom.

Breman, E., Gillson, L., Willis, K., 2012. How fire and climate shaped grass-dominated vegetation and forest mosaics in northern South Africa during past millennia. The Holocene 22, 1427–1439.

Bremond, L., Alexandre, A., Peiron, O., Guiot, J., 2005. Grass water stress estimated from phytoliths in West Africa. J. Biogeogr. 32, 311–317.

Bremond, L., Alexandre, A., Wooller, J.M., Hély, C., Williamson, D., Schäfer, A.P., Majule, A., Guiot, J., 2008. Phytolith indices as proxies of grass subfamilies on East African tropical mountains. Glob. Planetary Change 61, 209–224.

Bremond, L., Bodin, S., Bentaleb, I., Favier, C., Canal, S., 2017. Past tree cover of the Congo Basin recovered by phytoliths and δ 13 C along soil profiles. Quat. Int. 434, 91–101.

Brown, D.A., 1984. Prospects and limits of a phytolith key for grasses in the Central United-States. J. Archaeol. Sci. 11 (4), 345–368.

Cernusak, L.A., Ubierna, N., Winter, K., Holtum, J.A.M., Marshall, J.D., Farquhar, G.D., 2013. Environmental and physiological determinants of carbon isotope discrimination in terrestrial plants. New Phytol. 200, 950–965. https://doi.org/10.1111/nph.12423.

Clark, R.L., 1982. Point count estimation of charcoal in pollen preparations and thin sections of sediments. Pollen et Spores XXIV (3-4), 523–535.

Cordova, E.C., Scott, L., 2010. The potential of Poaceae, Cyperaceae and Restionaceae phtoliths to reflect past environmental conditions in South Africa. In: Runge, F. (Ed.), African Palaeoenvironments and Geomorphic Landscape Evolution. Taylor & Francis Group, Boca Raton, pp. 107–133.

Diester-Haas, L., Schrader, H.J., Thiede, J., 1973. Sedimentological and paleoclimatological investigations of two pelagic ooze cores off Cape Barbas, North-West Africa. Meteor Forsch-Ergebnisse C 16, 19–66.

Eshetu, Z., Hogberg, P., 2000. Reconstruction of forest site history in Ethiopian highlands based on ^{13}C natural abundance of soils. Ambio 29, 83–89.

Esteban, I., de Vynck, J.C., Singels, E., Vlok, J., Marean, C.W., Cowling, R.M., Fisher, E.C., Cabanes, D., Albert, R.M., 2017. Modern soil phytolith assemblages used as proxies for paleoscape reconstruction on the south coast of South Africa. Quat. Int. 434 B, 160–179.

Finsinger, W., Tinner, W., 2005. Minimum count sums for charcoal-concentration estimates in pollen slides: accuracy and potential errors. Holocene 15, 293–297.

Fredlund, G.G., Tieszen, L.T., 1994. Modern phytolith assemblages from the North American great plains. J. Biogeogr. 21 (3), 321–335.

Fredlund, G.G., Bousman, C.B., Boyd, D.K., 1998. The Holocene phytolith record from Morgan Playa in the rolling plains of Texas. Plains Anthropol. 43, 187–200.

Garnier, A., Neumann, K., Eichhorn, B., Lespez, L., 2013. Phytolith taphonomy in the middle-to late-Holocene fluvial sediments of Ounjougou (Mali, West Africa). The Holocene 23, 416–431.

Gibbs Russell, G.E., 1986. Significance of different centres of diversity in subfamilies of Poaceae in southern Africa. Palaeoecol. Afr. 17, 183–191.

Hammer, Ø., David, Harper A.T., Ryan, P.D., 2001. Past: paleontological statistics software package for education and data analysis. Palaeontol. Electron. 4 (1), 9 art. 4. 178kb. http://palaeo-electronica.org/2001_1/past/issue1_01.htm.

Harebottle, D., Eksteen, J., Linström, A., Krige, F., 2001. Site Information for Verloren Valei Nature Reserve, South Africa. Ramsar Sites Information Services http://ramsar.wetlands.org/Home/tabid/719/language/en-US/Default.aspx.

Holmgren, K., Lee-Thorp, J.A., Cooper, G.R.J., Lundblad, K., Partridge, T.C., Scott, L., Sithalden, R., Siep Talma, A., Tyson, P.D., 2003. Persistent millennial-scale climatic variability over the past 25,000 years in Southern Africa. Quat. Sci. Rev. 22, 2311–2326.

Holmgren, K., Risberg, J., Freudendahl, J., Achimo, M., Ekblom, A., Mugabe, J., Norström, E., Sitoe, S., 2012. Variations in precipitation during the last 2300 years at Lake Nhauhache, Mozambique. J. Palaeolimnol. 48 (2), 311–322.

Humphries, M.S, Green, A.N., Finch, J.M., 2016. Evidence of El Niño driven desiccation cycles in a shallow estuarine lake: the evolution and fate of Africa's largest estuarine system, Lake St Lucia. Glob. Planet. Chang. 147, 97–105.

Hyland, E., Smith, S.Y., Sheldon, N.D., 2013. Representational bias in phytoliths from modern soils of central North America: implications for paleovegetation reconstructions. Palaeogeogr. Palaeoclimatol. Palaeoecol. 374, 338–348.

Lajtha, K., Michener, R.H. (Eds.), 1994. Stable isotopes in ecology and environmental science. Methods in Ecology. Blackwell Scientific, Oxford xix, 316.

Lee-Thorp, J.A., Holmgren, K., Lauritzen, S.E., Linge, H., Moberg, A., Partridge, T.C., Stevenson, C., Tyson, P.D., 2001. Rapid climate shifts in the southern African interior throughout the mid to late Holocene. Geophys. Res. Lett. 28, 4507–4510.

Livingstone, D.A., Clayton, W.D., 1980. An altitudinal cline in tropical African grassfloras and its paleoecological significance. Quat. Res. 13, 392–402.

Lodder, J., Hill, T.R., Finch, J.M., 2018. A 5000-yr record of Afromontane vegetation dynamics from the Drakensberg Escarpment, South Africa. Quat. Int. 470, 119–129.

Madella, M., Alexandre, A., Ball, T., 2005. International code for phytolith nomenclature. Ann. Bot. 96, 253–260.

Meyers, P.A., 1994. Preservation of elemental and isotopic source identification of sedimentary organic matter. Chem. Geol. 114, 289–302.

Mucina, L., Geldenhuys, C.J., 2006. Afrotemperate, subtropical and azonal forests. In: Mucina, L., Rutherford, M.C. (Eds.), The Vegetation of South Africa, Lesotho and Swaziland. South African National Biodiversity Institute, Pretoria, pp. 584–615.

Mucina, L., Rutherford, M.C., 2006. The Vegetation of South Africa, Lesotho and Swaziland. South African National Biodiversity Institute, Pretoria.

Mulholland, S.C., 1989. Phytolith shape frequencies in North Dakota grasses: a comparison to general patterns. J. Archaeol. Sci. 16 (5), 489–511.

Neumann, K., Fahmy, A., Lespez, L., Ballouche, A., Huysecom, E., 2009. The early Holocene palaeoenvironment of Ounjougou (Mali): phytoliths in a multiproxy context. Palaeogeogr. Palaeoclimatol. Palaeoecol. 276, 87–106.

Neumann, F.H., Botha, G.A., Scott, L., 2014. 18,000 years of grassland evolution in the summer rainfall region of South Africa e evidence from Mahwaqa Mountain, KwaZulu-Natal. Veg. Hist. Archaeobot. 23, 665–681.

Norström, E., Scott, L., Partridge, T., Risberg, J., Holmgren, K., 2009. Reconstruction of environmental and climate changes at Braamhoek wetland, eastern escarpment South Africa, during the last 16,000 years. Palaeogeogr. Palaeoclimatol. Palaeoecol. 271, 240–258.

Norström, F., Neumann, F.H., Scott, L., Smittenberg, R.H., Holmstrand, H., Lundqvist, S., Snowball, I., Sundqvist, H.S., Risberg, J., Bamford, M., 2018. Late Quaternary vegetation dynamics and hydro-climate in the Drakensberg, South Africa. Quat. Sci. Rev. 105, 48–65.

Norström, E., Öberg, H., Sitóe, S.R., Ekblom, A., Westerberg, L.-O., Risberg, J., 2018a. Vegetation dynamics within the savanna biome in southern Mozambique during late Holocene. The Holocene https://doi.org/10.1177/0959683617721327.

Norström, E., Norén, G., Smittenberg, R.H., Massuanganhe, E.A., Ekblom, A., 2018b. Leaf wax δD inferring variable medieval hydroclimate and early initiation of Litte Ice Age (LIA) dryness in southern Mozambique. Glob. Planet. Chang. 170, 221–233.

Novello, A., Barboni, D., Berti-Equille, L., Mazur, J.C., Poilecot, P., Vignaud, P., 2012. Phytolith signal of aquatic plants and soils in Chad, Central Africa. Rev. Palaeobot. Palynol. 178, 43–58.

Novello, A., Barboni, D., Sylvestre, F., Lebatard, A.-E., Paillès, C., Bourlès, D.L., Likius, A., Mackaye, H.T., Vignaud, P., Brunet, M., 2017. Phytoliths indicate significant arboreal cover at *Sahelanthropus* type locality TM266 in northern Chad and a decrease in later sites. J. Hum. Evol. 106, 66–83.

Parker, A.G., Eckersley, L., Smith, M.M., Goudie, A.S., Stokes, S., Ward, S., White, K., Hodson, M.J., 2004. Holocene vegetation dynamics in the northeastern Rub' al-Khali desert, Arabian Peninsula: a phytolith, pollen and carbon isotope study. J. Quat. Sci. 19, 665–676.

Parr, J.F., Lentfer, C.J., Boyd, W.E., 2001. A comparative analysis of wet and dry ashing techniques for the extraction of phytoliths from plant material. J. Archaeol. Sci. 28 (8), 875–886.

Parr, C.L., Lehmann, C.E., Bond, W.J., Hoffmann, W.A., Andersen, A.N., 2014. Tropical grassy biomes: misunderstood, neglected, and under threat. Trends Ecol. Evol. 29, 205–213.

Piperno, D.R., 2006. Phytoliths: A Comprehensive Guide for Archaeologists and Paleoecologists. Altamira Press, Lanham, Maryland.

Rossouw, L., 2009. The application of fossil grass-phytolith analysis in the reconstruction of late Cainozoic environments in the South African interior. Doctoral Thesis. University of the Free State, Bloemfontein, South Africa, pp. 1–317.

Runge, F., 1999. The opal phytolith inventory of soil in central Africa – quantities, shapes, classification, and spectra. Rev. Palaeobot. Palynol. 107, 23–53.

Rutherford, M.C., Mucina, L., Powrie, L.W., 2006a. Biomes and bioregions of southern Africa. In: Mucina, L., Rutherford, M.C. (Eds.), The Vegetation of South Africa, Lesotho and Swaziland. South African National Biodiversity Institute, Pretoria, pp. 30–51.

Rutherford, M.C., Mucina, L., Lotter, M., Bredenkamp, G.J., Smit, J.H.L., Scott-Shaw, C.R., Hoare, D.M., Goodman, S., Bezuidenhout, H., Scott, L., Ellis, F., Powrie, L.W., Siebert, F., Mostert, T.H., Henning, B.J., Venter, C.E., Kelson Camp, G.T., Siebert, S.J., Matthews, W.S., Burrows, J.E., Dobson, L., van Rooyen, N., Schmidt, E., Winter, P.J.,

du Ptretz, J., Ward, R.A., Williamson, S., Hurter, P.J., 2006b. Savanna biome. In: Mucina, L., Rutherford, M.C. (Eds.), The Vegetation of South Africa, Lesotho and Swaziland. South African National Biodiversity Institute, Pretoria, pp. 439–538.

Scott, L., 1990. Environmental changes reflected by pollen in some Holocene sediments from Transvaal, South Africa and Marion Island, Southern Ocean. S. Afr. J. Sci. 86, 464–466.

Scott, L., Lee-Thorp, J., 2004. Holocene climatic trends and rhythms in southern Africa. In: Batterbee, R.W., Gasse, F., Stickley, C.E. (Eds.), Past climate variability through Europe and Africa. Springer, Dordrecht, pp. 69–91.

Scott, L., 2016. Fluctuations of vegetation and climate over the last 75 000 years in the Savanna Biome, South Africa: Tswaing Crater and Wonderkrater pollen sequences reviewed. Quat. Sci. Rev. 45, 117–133.

Scott, L., Holmgren, K., Partridge, T.C., 2008. Reconciliation of vegetation and climatic interpretations of pollen profiles and other regional records from the last 60 thousand years in the Savanna Biome of Southern Africa. Palaeogeogr. Palaeoclimatol. Palaeoecol. 257, 198–206.

Scott, L., Neumann, F.H., Brook, G.A., Bousman, C.B., Norström, E., Metwally, A.A., 2012. Terrestrial fossil-pollen evidence of climate change during the last 26 thousand years in Southern Africa. Quat. Sci. Rev. 32, 100–118.

Sjöström, J., Norström, E., Risberg, J., Schoeman, M.H., 2017. Late Holocene palaeoenvironmental reconstruction from Mpumalanga, South Africa, derived from biogenic and geochemical proxies. Rev. Palaeobot. Palynol. 246, 264–277.

Smith, J.M., Lee-Thorp, J.A., Sealy, J.C., 2002. Stable carbon and oxygen isotopic evidence for late Pleistocene to middle Holocene climatic fluctuations in the interior of southern Africa. J. Quat. Sci. 17 (7), 683–695.

Strömberg, C.A.E., 2009. Methodological concerns for analysis of phytolith assemblages: does count size matter. Quat. Int. 193 (1–2), 124–140.

Strömberg, C.A.E., Werdelin, L., Friis, E.M., Sarac, G., 2007. The spread of grassdominated habitats in Turkey and surrounding areas during the Cenozoic: phytolith evidence. Palaeogeogr. Palaeoclimatol. Palaeoecol. 250 (1–4), 18–49.

Sundqvist, H.S., Holmgren, K., Fohlmesiter, J., Zhang, Q., Bar Matthews, B., Spötl, C., Körnich, H., 2013. Evidence of a large cooling between 1690 and 1740 AD in southern Africa. Sci. Rep. 3, 1767.

Talbot, M.R., Laerdal, T., 2000. The Late Pleistocene – Holocene palaeolimnology of Lake Victoria, East Africa, based upon elemental and isotopic analyses of sedimentary organic matter. J. Paleolimnol. 23, 141–164.

Tieszen, L.L., Senyimba, M.M., Imbamba, S.K., Troughton, J.H., 1979. The distribution of C$_3$ and C$_4$ grasses and carbon isotope discrimination along an altitudinal and moisture gradient in Kenya. Oecologia 37, 337–350.

Twiss, P.C., 1992. Predicted world distribution of C3 and C4 grass phytolihs. In: Rapp Jr., G., Mulholland, S.C. (Eds.), Phytolith Systematics. Emerging Issues, Advances in Archaeological and Museum Science. Vol. 1. Plenum Press, pp. 113–128.

Twiss, C.P., Suess, E., Smith, R.M., 1969. Morphological classification of grass phytoliths. Soil Sci. Soc. Am. 33, 109–115.

Vogel, J.C., Fuls, A., Ellis, B.P., 1978. The geographical distribution of Kranz Grasses in South Africa. S. Afr. J. Sci. 74, 209–215.